ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

May 2007 **Volume 25, N° 1-2**

Alytes, 2007, **25** (1-2): 1-37.

Zoogeography of the treefrogs in Africa's tropical forests

Arne SCHIØTZ

Humlehaven 2, 4571 Grevinge, Denmark
<arne@schiotz.dk>

The zoogeographical patterns of the forest faunas of treefrogs (Hyperoliidae and genus *Leptopelis*) in tropical Africa are analysed. This group is well-suited for such a work since especially the genus *Hyperolius* shows great diversification and signs of recent speciations. For the purpose of this analysis, the species are separated into sylvicolous ("high forest") and parasylvicolous ("farmbush"). The forests in this study are tentatively divided into ten forest blocks based on differences in the treefrog fauna, and such differences are analysed.

The sylvicolous species of the genus *Hyperolius* have a distribution pattern with a total separation at species level between forest blocks which may reflect the division of the forest belt through drier periods of late Pleistocene into a number of isolated refugia where moist forest and its fauna have persisted and may have resulted in allopatric speciation. The genera *Afrixalus* and *Leptopelis* show less diversification since the sylvicolous species of these genera are separated into three regions, or groups of forest blocks, with groups of species common for these regions, but with no species common between these regions, and only slightly overlapping in southern Nigeria. These regions are West Africa west of the Dahomey Gap/Nigeria, Central Africa and the Eastern Forests.

The parasylvicolous species show a fundamentally different distribution pattern. One group is found in West Africa and in Central Africa along the Atlantic coast but not far inland. Another group is found in Central Africa, including Cameroun and easternmost Nigeria and the forest block along the Atlantic coast. Finally one group is widely distributed in the dry parts of the Eastern Forests. The three groups are separated at species level, but the former two have a considerable area of geographical overlap along the Atlantic coast of Central Africa from Cross river southwards. The distribution of the parasylvicolous fauna does not show well-defined "faunal breaks" similar to the sylvicolous fauna, but species diversification and distinction between vicariant taxa seem to have taken place at different, apparently "random" places, perhaps reflecting the original, linear distribution of this fauna in a narrow forest edge towards the savanna.

The ill-delimited orophile treefrog faunas are found in three areas with full separation at species level: Mount Cameroun and the Cameronese ridge; the mountains in Central Africa (Albertine Rift and adjacent highlands); and the Eastern Arc Mountains.

A recent proposal that the species structure in the genus *Hyperolius* can be traced back to Cretaceous is discussed. It is argued that climatic changes in late Pleistocene are sufficient to explain the present species structure.

Introduction

It can be argued that the exploration of Amphibia in tropical Africa is still so fragmentary that a comprehensive zoogeographical analysis is premature – or that attempts to perform such an analysis, even on an incomplete background, are useful as an inspiration for further studies. Such an attempt is presented here, based on many years of fieldwork in tropical Africa, and on the taxonomical work of many authors (compilation in Schiøtz, 1999).

The aim of the present paper is to analyse the zoogeographical patterns of the forest faunas of treefrogs in tropical Africa. For the analysis, these forest-related faunas are divided into two groups relating to their habitat, generally sympatric but not syntopic, i.e. sylvicolous (high forest) and parasylvicolous (farmbush/bushland) species.

Treefrogs are here defined as the group conventionally termed the family Hyperoliidae, although recent studies (Frost et al., 2006) indicate that the genus *Leptopelis* does not belong in this group (see app. 1). The mainly Asian treefrog family Rhacophoridae has only one forest related member in Africa, *Chiromantis rufescens*, but there is some doubt (Rödel, in litt.) whether populations from western and central Africa are conspecific. This species is therefore not treated further here.

The present attempt to base a zoogeographical treatment on ecological divisions is inspired by studies from West Africa (Schiøtz, 1967) of the three clearly separate lowland faunas, associated with savanna, high forest and farmbush respectively. Among them, especially the latter is sympatric but rarely syntopic with the former two. It was shown in the West African study that these three faunas show three clearly different distribution patterns: the savanna-living species are generally widely distributed throughout the West African savanna and further East, often stretching to western Ethiopia and Uganda, the high forest species are clearly localised to "forest islands", today partly confluent, and the farmbush fauna has a wide distribution, with tendencies to subspecific or specific splitting up at apparently "random" places throughout West Africa.

The paper is an attempt to carry out a similar analysis for the entire forest belt of tropical Africa, and more specifically to address a number of questions, such as: (1) is there a basic difference in the zoogeographical pattern of the two proposed "faunas", sylvicolous and parasylvicolous, making it relevant to analyse the two faunas separately?; (2) what are the zoogeographical patterns for the two faunas?; (3) what is a possible explanation for these patterns?

A problem with the present treatment based on an ecological division is that a direct comparison with Poynton's several papers (e.g. Poynton's 1999 benchmark paper) is difficult, since his approach, without a clear distinction between the faunas, tends to obscure part of what I see as the distinctness of the biogeographical regions and blocks.

The African treefrogs are deemed suitable for such a study because: (1) their distribution is reasonably well known on a continental scale; (2) the taxonomy of the forest-related species is reasonably settled; (3) so are their habitat preferences; (4) they show signs of recent speciation; (5) they contain a sufficiently large number of taxa for analysis.

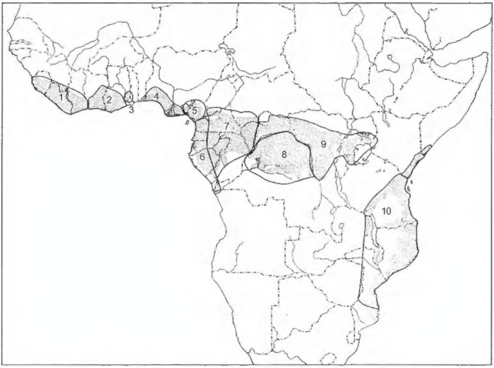


Fig. 1. – Division into forest blocks.

The dotted areas on the map represent for West- and Central Africa moist, evergreen forest (rainforest) as climax vegetation. In Eastern Africa such areas represent rainforest in the Eastern Arc as well as dry, semideciduous forest inhabited by the parasylvicolous fauna.

The numbers refer to forest blocks (see text): 1, Liberia; 2,: Gold Coast; 3, Trans-Volta-Togo; 4, Southern Nigeria; 5, Cross-Sanaga Coastal Forests; 6, Congolian Coastal Forests; 7, North-western Congolian Forests; 8, Central Congolian Forests; 9, North-eastern Congolian Forests; 10, Eastern Forests.

Our knowledge of the distribution of the Amphibia in the forest regions of Africa spreads from very good (Cameroun, western Côte d'Ivoire, Eastern forests) to grossly inadequate (much of the Congo basin).

The taxonomic knowledge of most treefrog genera is fair in the way that they have been subjected to rather recent treatments over large areas – sometimes continent-wide – although it can be argued that a thorough systematical treatment based on DNA, which will give us a deeper understanding of the phylogenetic relationships, has just started, and has until now been so sporadic that the conclusions drawn can be disputed.

The level of knowledge of the two faunas, parasylvicolous and sylvicolous, is very different. The conspicuous and easily accessible parasylvicolous fauna tends to be well-known, whereas the sylvicolous fauna is incompletely known until searched for by experienced collectors, seeking unconventional and sometimes inaccessible places and finding the

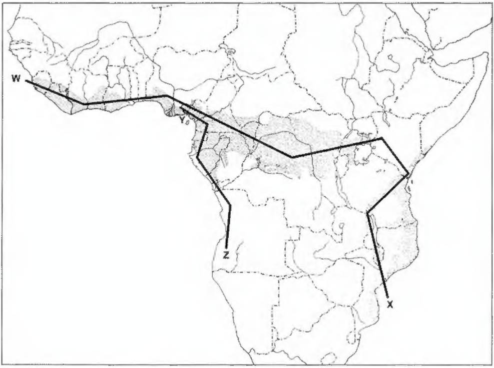


Fig 2. – Transect lines used in tables 1-4.

few and scattered specimens guided by their voices. The rule is therefore that the sylvicolous fauna tends to have been recently described and that new discoveries are mainly made in this group.

Although most taxa treated here are known from a reasonable number of localities, the exact borders of their distribution are often guesswork. For the parasylvicolous fauna, in most cases we have a satisfactory density of records, and furthermore often sets of allopatric taxa – sometimes regarded as subspecies – replacing each other in a way we interpret as vicariance, not only geographically but also ecologically. The sylvicolous fauna is more difficult. A number of species were recorded only from part of the proposed ecoregion. Sometimes it is because only this part has been thoroughly searched, sometimes because the species may be confined to a wetter, "richer" core area. Both explanations seem valid for the rich fauna of western Côte d'Ivoire, the part of the forest block with most rainfall, but also by far the best explored forests in the Liberia block. The richness of the faunas of southern Cameroun compared to areas to the East and South may mainly be due to the thorough collecting effort here. A consequence of this uncertainty – not likely to be solved in the near future – is that whereas the distinction between faunas of the forest blocks can be assessed, the identification of the exact borders between them, especially in Central Africa, must be left open.

Table 1. – Distribution of sylvicolous taxa, from Sierra Leone to the Indian ocean, along transect W-X (fig. 2).

The numbers refer to forest blocks (see text and fig. 1): 1, Liberia; 2,: Gold Coast; 3, Trans-Volta-Togo; D: Dahomey Gap; 4, Southern Nigeria; 5, Cross-Sanaga Coastal Forests; 6, Congolian Coastal Forests; 7, North-western Congolian Forests; 8, Central Congolian Forests; 9, North-eastern Congolian Forests; A, Arid Corridor; 10, Eastern Forests. FN, Footnotes. Note that block 8 breaks the linear sequence. +++, widely distributed within the block; ++, collection effort insufficient to show distribution; +, only known from very restricted range in spite of ample collection; C, Central; E, East; N, North, S, South; W, West. Abbreviations of generic names in this table and next ones: *A*, *Afrixalus*; *Ac*, *Acanthixalus*; *Al*, *Alexteroon*; *Ar*, *Arlequinus*; *C*, *Callixalus*; *Ch*, *Chlorolius*; *Cr*, *Cryptothylax*; *H*, *Hyperolius*; *K*, *Kassina*; *L*, *Leptopelis*; *O*, *Opisthothylax*; *P*, *Phlyctimantis*.

Species name	1	2	3	D	4	5	6	7	8	9	A	10	FN
H. chlorosteus	+++												
H. zonatus	+++												
H. wermuthi	+												
H. nienokouensis	+												
K. lamottei	+												
Ac. sonjae	++	++											
L. macrotis	+++	+++											
A. vibekensis	+	+											
H. viridigulosus	E	+++											
H. laurenti		+++											
H. bobirensis		++											
L. occidentalis	+++	+++			?								1
A. nigeriensis	+++	+++			+++								
H. torrentis			++										
L. brevirostris					++	+++	N						
O. immaculatus					++	+++	N	++					
L. boulengeri					?	+++	++	?	?	?			1-2
Al. jynx						+							
H. bopeleti						S	N						3
A. schneideri						?							
Ar. krebsi						++							
L. modestus						+++							4
Ch. koehleri						+++	N						
H. acutirostris						+++	N						
L. rufus						+++	+++						
H. endjami						+++	+++						
Al. hypsiphonus						+++	+++	++					
Al. obstetricans						+++	+++	++					
L. omissus						+++	+++	++					
L. crystallinoron							++						
L. zebra							N	++					

1. Records from western Nigeria refer either to *L. occidentalis* or to *L. boulengeri* (SCHIØTZ, 1967).
2. Records from blocks 7-9 (LAURENT, 1973) are doubtful.
3. Erroneously termed a bushland species by SCHIØTZ (1999) (AMIET, in litt.).
4. Doubtful records further east.

Table 1 (continued).

Species name	1	2	3	D	4	5	6	7	8	9	A	10	FN
H. mosaicus							N	N					
H. ghesquieri								++					
L. o. schiotzi									++				
L. c. meridionalis									+++				
A. equatorialis									+++	+++			
A. laevis						+++	+++	+++	++	+++			
H. ocellatus						+++	+++	+++	++	+++			
Ac. spinosus						+++	+++	++		+++			
L. millsoni						+++	+++	+++	++	+++			
L. c. calcaratus						+++	+++			+++			
L. o. ocellatus							+++			+++			
A. leucostictus									?	+++			
C. pictus										+			5
H. leleupi										+			5
H. frontalis										+			6
H. alticola										+			6
L. kivuensis										+			6
A. uluguruensis												+++	
L. parkeri												+++	
L. barbouri												+++	
L. vermiculatus												+++	
L. uluguruensis												+++	
H. tannerorum												N	
H. kihangensis												C	
TOTAL	11	8	1		3 (5)	19 (20)	20	11 (12)	6 (8)	13* (14)		7	

5. Montane, endemic to the Itombwe Plateau.
6. Montane, endemic to the Albertine rift mountains.
* Five species from the Albertine rift mountains omitted (see text).

Extrapolation of the distribution brings an element of subjectivity into this study. I believe this to be defensible especially in the many cases where vicariant taxa replace each other. But there is a danger that preconceived ideas about the zoogeographical units filter into published range maps, thus making appear legitimate what is in fact only a working hypothesis.

Methods

Detailed taxonomic information on taxa are not provided here. Appendix 1 gives the complete list of taxa mentioned in the text, with their authors and dates and their taxonomic allocation (in families, genera, species and subspecies) according to Frost et al. (2006). Some recent information can be found in Schiotz (1999), Rödel et al. (2003), Amiet (2000, 2001, 2004*b*, 2005), Lötters & Schmitz (2004), Dubois et al. (2005), Lötters et al. (2005) and Köhler et al. (2006).

Table 2. – Distribution of sylvicolous taxa, from Cross river to Angola, along transect Y-Z (fig. 2). In order to seek maximal resolution, in this table forest block 6 is subdivided after the lines shown on fig. 8. The area between lines F and G is block 5, that between G and K is block 6. FN, footnotes. For other abbreviations, see legend of tab. 1.

Species name	F–G	G–H	H–I	I–J	J–K	K–L	FN
Al. jynx	+						
Ar. krebsi	++						
A. schneideri	?						
H. acutirostris	+++	+					1
H. bopeleti	S	+					1
H. endjami	++	+++					1
H. mosaicus		+					2
A. laevis	+++	+++					3
L. zebra		(+)					4
L. crystallinoron			+				
Ch. koehleri	+++	++	++				
L. brevirostris	+++	+++	++				2
O. immaculatus	+++	+++		++			2
L. millsoni	+++	+++	++	++			3
L. calcaratus	+++	+++	++	++			3
L. rufus	+++	+++	++	++	++		1
Al. obstetricans	+++	+++	++	++	++		2
L. boulengeri	+++	+++	++		++		2
Al. hypsiphonus	+++	+++	++	++	++		2
L. omissus	+++	+++	++	++	++		2
Ac. spinosus	+++	+++		++	++		3
L. ocellatus		E	++	++	++		3
H. ocellatus	+++	+++	++	++	++		3
TOTAL	18 (19)	19	12*	10	8	0	

1. Confined to block 5 and (part of) block 6.
2. Also in south-eastern Cameroun, and presumably further east in block 7.
3. Also further east in the Congo Basin.
4. Distribution badly known. Found in south-eastern Cameroun, one record touches present area.
* BURGER et al. (in press) listed 30 treefrogs from south-western Gabon (sector I-J in present paper), including 7 or 9 unidentified species, but presented no information about habitat preference.

The forest-related treefrogs in tropical Africa are divided into sylvicolous and parasylvicolous species as further elaborated on pages 10-12 and in tables 1-4. A search for clusters in their distribution was undertaken. The result is that the parasylvicolous fauna does not fall into well-defined clusters, but the sylvicolous fauna does. Partly based on such clusters of sylvicolous species and partly based on recognized zoogeographical entities characterized by distribution of other animals (OLSON & DINERSTEIN, 1998), the forest was tentatively divided into ten forest blocks (p. 12). An attempt was made to characterize these forest blocks by their treefrog fauna and to assess the validity and significance of the blocks.

An attempt was made to make a hierarchical dendrogram illustrating the similarity between the sylvicolous treefrog faunas in the forest blocks using the Quotient of Similarity

(QS) (Sørensen, 1948): 2 × number of taxa common to both areas, divided by sum of totals of taxa from both areas × 100 (see p. 20 and fig 6).

The statement of close affinity between habitat and fauna is based on numerous observations of animals at the breeding site. Anecdotal evidence points at a less rigorous affinity outside the breeding season, where, however, observations are scarce.

The distribution data are taken from many sources, mostly compiled in Schiøtz (1999).

Why treefrogs?

It has been shown earlier in a study from West Africa (Schiøtz, 1967) that the treefrogs seem well suited for a zoogeographical analysis, in fact better than other Amphibia. Especially the genus *Hyperolius*, which seems to be in a process of recent speciations, shows a finer geographical separation at the species- or subspecies-level through West Africa than most or all other genera. The genera *Afrixalus* and *Leptopelis* show less splitting-up, but still a significant one. Genera in other families are less suited for such an analysis, sometimes because their taxonomy is far less understood. For instance, the large genera *Phrynobatrachus* and *Arthroleptis* (only surpassed by *Hyperolius* in number of species), suffer from an unsettled taxonomy. To measure with confidence the level of taxonomic uncertainty is hardly possible, and is not always apparent from published fauna-lists, but an indication of the uncertainty is that J.-L. Amiet, a most meticulous worker in the best explored country in tropical Africa, Cameroun, only lists 3 certain names in the genus *Arthroleptis* out of a total of 12 species occurring in that country, and only 8 certain names out of 20 species of *Phrynobatrachus* (Amiet, pers. comm.). Such reservations, even from a very well-explored area, make the genera unsuited for continent-wise zoogeographical analyses. Amiet in comparison lists none of the 24 *Hyperolius* and none of the 16 *Leptopelis* taxa as taxonomically unsettled.

The two faunas in the Afro-tropical forest

As generally acknowledged, two well-defined faunas of Amphibia co-exist in the forest belt, sympatric but normally not syntopic. The first one is, at least in the breeding season and on breeding sites, strictly confined to reasonably undisturbed closed-canopy forests and has been termed the High Forest Fauna (Schiøtz, 1967, 1975, 1999). The other is confined to disturbed, often heavily disturbed forest, cultivated clearings in forests, dry forests and well-developed gallery forests in the humid savanna. The name Farmbush Fauna was used in Schiøtz, (1967, 1975) for this fauna, changed to the Bushland Fauna in Schiøtz (1999). The change, which may have been unfortunate, was undertaken because several colleagues, mainly those not familiar with the tropical moist lowland forests of Africa, had difficulties with the distinction between the two faunas and in understanding the name farmbush which

Table 3 Distribution of parasylvicolous taxa from Sierra Leone to Angola, along transect W-Y-Z (fig. 2). Capital letters refer to "breaks" (see fig. 8) as distinct from the forest blocks of table 1. EW and EE delimit the Dahomey Gap. FN, footnotes. For other abbreviations, see legend of tab. 1.

Species name	A	B	C	D	Ew	Ee	F	G	H	I	J	K	L	FN
H. occidentalis	+++													
H. nimbae		E												1
K. cochranae		+++												
K. arboricola			+++	+++										
P. boulengeri W		+++	+++	W										2
H. picturatus		+++	+++	+++										
H. baumanni					+++									
H. f. fusciventris	+++	+++												3
H. f. lamtoensis			+++	?										3
H. f. burtoni				+++	+++		+++							3
H. f. ssp.								+++						3
L. hyloides	+++	+++	+++	+++	+++		+++							
H. c. concolor		+++	+++	+++	+++									
H. c. ibadanensis							+++							
H. c. ssp								+++						
H. s. ivorensis			+++											
H. s. sylvaticus				+++										
H. s. nigeriensis							+++	+++						
H. guttulatus		+++	+++	+++			+++	+++	+++		++			
A. d. dorsalis		+++	+++	+++	+++		+++	+++	+++					
A. d. regularis										++	++	++	++	
P. boulengeri E							E	+++	+++					2
H. tuberculatus							E	+++	+++	++	++			
A. lacteus								+						4
H. r. riggenbachi								+						4
H. r. hieroglyphicus								+						4
H. camerunensis								C						5
L. notatus								+++	+++	++	++			
H. bolifambae								+++	+++					
H. kuligae								+++	+++					6
A. paradorsalis								+++	++	++	++			
H. dintelmanni									+					
H. pardalis									+++	+	++			
L. aubryi								++	+++	++	++	++		
H. phantasticus									+++		++	++		
H. platyceps									+++	++	++	++		
H. adspersus								+	++		++	++	++?	7
P. leonardi										++	++	++		
Cr. greshoffii										++	++	++		
H. cinnamomeoventris									+++	+	++	++	++	
A. osorioi													++	
TOTAL	3	9	9	9 (10)	5		8	17	15	10	13*	8	3 (4)	

1 Known only from a very small area near cutting line B
2 The widely separated *P. boulengeri* East and West are here treated as separate taxa
3 Possibly separate, vicariant species (RÖDEL & ERNST, 2003, RÖDEL et al., 2005)
4 Largely montane, endemic to the Cameronese ridge
5 Confined to a small area in Cameroun
6 Doubtful Uganda record
7 Distribution virtually unknown due to confusion with "*H. nasutus*"
* BURGER et al. (in press) listed 30 treefrogs from south-western Gabon (sector IJ in present paper), including 7 or 9 unidentified species, but presented no information about habitat preferences

Table 4. – Distribution of parasylvicolous taxa, from Cross river to the Indian ocean, along transect Y-X (fig. 2).

Only species ocurring east of Cross river are included. For species further west, see table 3. Numbers refer to forest blocks (fig. 4) since data are too incomplete to suggest dividing breaks. Block 6 is only touched in its northern part. Blocks 7, 8 and 9 do not form a linear sequence. For other abbreviations, see legend of tab. 1.

Species name	5	6	7	8	9	A	10	FN
H. fusciventris	+++							1
H. concolor	+++							1
H. sylvaticus	+++							1
H. bopeleti	+++							
A. lacteus	+							2
H. r. riggenbachi	+							2
H. r. hieroglyphicus	+							2
H. camerunensis	+							
H. guttulatus	+++	++						3
A. dorsalis	+++	+++						3
P. boulengeri E	+++	N						
H. dintelmanni		+						
A. paradorsalis	+++	+++	W					
H. bolifambae	+++	+++	W					
L. aubryi	+++	+++	++					
H. adspersus	+	+++	W					4
H. kuligae	+++	+++	W					
H. pardalis		+++	++					
P. leonardi		S	W	W				
H. platyceps		+++	W	++				
L. notatus	+++	+++	+++	+++				
H. phantasticus		+++		+++				
C. greshoffii		+++	+++	+++				
H. tuberculatus	+++	+++	+++	+++	+++			
H. cinnamomeoventris		+++	+++	++	+++			
L. christyi			?		+++			5
A. osorioi			E	+++	+++			
K. mertensi				+	+++			
H. robustus				++	+			
P. verrucosus				+++	+++			
L. fiziensis					++			
H. hutsebauti					+			
H. castaneus					+			6
H. lateralis					+++			
L. mackayi					E?			7
H. kivuensis					+++			8
H. puncticulatus							+++	
H. mitchelli							+++	
L. flavomaculatus							+++	
H. rubrovermiculatus							N	
A. sylvaticus							N	
P. keithae							+	9
TOTAL	18	17	13 (14)	11	13		6	

1. Also occurring further west (table 3).
2. Montane, endemic to the Cameronese ridge.
3. Occurring further west and south (table 3).
4. Distribution badly known.
5. Cameronese populations may belong to a different taxon (AMIET, 2004a).
6. Montane from Albertine rift mountains.
7. Only known from western Kenya, possibly also in Republique Democratyque du Congo.
8. Also dense savanna south of forest belt.
9. Habitat preference badly understood.

is meaningless in the savanna and dry forests where farmed or degraded land harbour the same fauna as unfarmed land. To avoid such misunderstandings, I will instead use terms which may give fewer associations, namely *sylvicolous* for the High Forest Fauna, and *parasylvicolous* for the Farmbush/Bushland fauna, names proposed by AMIET (1989) – in French as *sylvicole* and *parasylvicole* – in addition to the term *savanicolous* for the savanna-living forms.

It was shown for West Africa (SCHIØTZ, 1967) and for Eastern Africa (SCHIØTZ, 1976, 1981) that the zoogeographical patterns for the sylvicolous and the parasylvicolous faunas differ profoundly from each other (and both differ profoundly from the pattern of the savanna fauna), so that the most "precise", and therefore most informative picture is obtained by keeping these faunas separate. This is therefore also done in this study.

The 103 forest-related treefrog species – 115 taxa when considering recognized subspecies – suited for analyses can be separated into 49 parasylvicolous and 54 sylvicolous species, or 59/56 when subspecies are considered, plus a few excluded species (app. 3). Since the separation into the geographically largely overlapping sylvicolous and parasylvicolous faunas can only be undertaken based on a thorough field-knowledge of the forms, there is a certain element of subjectivity in this separation and it can hardly be expected that workers in different parts of the forest belt agree completely on the distinction between sylvicolous and parasylvicolous species. It might, however, be relevant to compare this distinction in two comparable areas covered by different workers, namely the rather well-investigated West Africa west of the Dahomey Gap (mainly Schiøtz and Rödel, compilation in SCHIØTZ, 1999 and RÖDEL, 2000) and the very well investigated Cameroun (mainly Mertens, Perret and Amiet, compilation in PERRET, 1966 and AMIET, pers. comm.). West Africa has 14 species of sylvicolous treefrogs, 13 parasylvicolous; Cameroun has 22 and 23 respectively. These ratios could indicate that the distinction between the two faunas by the two set of workers is congruent, supported by the fact that Amiet's and my references to habitat type for the species we both know from the field is identical.

Practical field experience is deemed necessary. The division in this paper is thus based on the author having encountered 81 of the 115 treated taxa in the field, supplemented with Amiet's field experience of an impressive 46 taxa out of a total of 48 in Cameroun, of which 21 have not been encountered in the field by me (AMIET, 1986 and in litt.). Habitat preference for the taxa encountered neither by Amiet nor by me is given by a number of other authors, accepted here since there is no disagreement with these authors' general allocation of species to habitat. A compilation of data for distribution and habitat preference is found in SCHIØTZ (1999), supplemented with data found in the description of more recently described species (see DUBOIS et al., 2005). Only a recent paper by WIECZOREK et al. (2000) differs profoundly from the present paper in its allocation of *Hyperolius* to habitat (discussed further p. 30). In spite of his many years in Africa, Laurent, the authority on the African treefrogs, only rarely mentioned habitat affinity in his papers.

It should be noted that the habitat affinity, even of the rarer taxa of which only few specimens have been collected, is normally based on many records of voices where the collectors especially would investigate frogs calling from an unusual place. Exceptions from the habitat affinity should therefore be stressed rather than downplayed by our collecting methods. Since it is to be expected that every species has its own ecological requirements and preferences it is not surprising that some species do fall outside this rigorous division, sometimes perhaps because of a broader requirement, sometimes perhaps by requirements not expressed by the sylvicolous/parasylvicolous division. Such species are dealt with in appendix 3.

Amiet has in his later papers (first Amiet, 2001) introduced the term *phonocénose* for the "sound-scape" in which the calling males are found, "des ensembles d'espèces qui exercent leur activité vocale... pendant la même période de l'année et dans des sites présentant des caracteristiques écologiques similaires". He uses this concept in addition to, not replacing, his distinction between sylvicolous and parasylvicolous species. This term is perhaps a more precise definition of what I have called "faunas", for strictly speaking we know very little of the affinity to the vegetation outside the breeding season and breeding sites. Very few specimens are collected outside the breeding season and breeding sites, and there is some anecdotal evidence that some migration through "alien" vegetation occurs, at least for savanicolous and parasylvicolous species (Schiotz & Daele, 2003: 143; Amiet, in litt.). On the other hand, the term phonocénose may be too narrow for the present purpose since, at least within the sylvicolous species, some are connected with small streams, others with small stagnant swamps, etc. They may not belong to the same phonocénose, but are here regarded as belonging to the same fauna. Also the timing of breeding activity in the rainy season may separate species belonging to the same fauna into different phonocénoses.

Poynton, in several papers, expressed some reservation as to the link between Amphibia distribution and vegetation (e.g., Poynton, 1962: 34: "large-scale faunal patterning which is determined mainly by the vegetation patterning should be treated with a great deal of caution"). My approach, however, is to regard affinity to the vegetation types as the fundamental basis for the distribution of the species. We do not know specifically which factors are decisive, but field observation (not only of frogs) demonstrates clearly this dependence, and it is extremely rare to find specimens in "the wrong vegetation". Microclimate, so dramatically different especially between savanna and closed canopy forest, may be one factor. This could explain Poynton's (2000*b*) observation that species which are forest-limited in lowlands, sometimes occur in open formations at high altitude.

The smallest recognised systematical unit, subspecies, is used in this paper. It is noteworthy that no cases are known of different subspecies within a species occupying different habitats. Habitat affinity seems to be a fundamental species character. The two faunas, sylvicolous and parasylvicolous, are thus taxonomically separate at species level, and are approximately of similar magnitude of species diversity in any given area.

Forest blocks

A basis for the present study is the forest ecoregions proposed by the World Wildlife Fund (WWF) in their "Global 200" study (Olson & Dinerstein, 1998). WWF's division into ecoregions is a consensus result of wide consultations with workers familiar with different animal and plant groups. An ecoregion is defined by WWF as "a geographically distinct assemblage of natural communities that share a large majority of their species, ecological dynamics and environmental conditions". This division differs somewhat from that proposed by POYNTON (1999), whose definition of regions is more pragmatic "a region is... an area covered by a perceived set of species ranges". Another definition – even more pragmatic is that of NOBLE (1924. 152) for his biogeographical regions: "convenient areas for distributional discussion".

Since several of WWFs ecoregions invite to further subdivision when looking at the fauna of treefrogs, several of them has been subdivided in this paper into forest blocks based on a perceived set of species ranges. In this paper, the term forest block is used for all the units studied here. Unfortunately, the terminology for blocks used here is not directly comparable with the divisions in POYNTON (1999) (app. 2).

THE SYLVICOLOUS FAUNA

DISTRIBUTION

In this study, ten forest blocks (fig 1) are tentatively recognised as a basis for discussion of the distribution of the sylvicolous fauna. They are a result of my analyses of the distribution of the sylvicolous fauna. The parasylvicolous fauna has not contributed to their characterization. The validity and significance of these blocks are described and discussed in this and the following chapter and tables 1-2.

Block 1. Liberia Block

Distribution. – From western Guinea, western Senegal and Sierra Leone to V baole which is a tongue of savanna stretching almost to the coast along Bandama river in eastern Côte d'Ivoire.

Knowledge. – Well explored (LAURENT, 1958, GUIBÉ & LAMOTTE, 1958; RÖDEL, 2000, SCHIØTZ, 1967).

Description. - Forest degraded and fragmented. The westernmost part (western half of Sierra Leone, western Guinea and Senegal) seems to harbour a dry part of the forest with only one sylvicolous species, *Hyperolius chlorosteus*, recorded. The parasylvicolous fauna it this part is distinctive (p. 26).

Endemics. – *Hyperolius chlorosteus*; **H. nienokouensis*, *H. wermuthi*, *H. zonatus*, **Kassina lamottei*. Species marked with * are only recorded from the central part of the region.

Block 2. Gold Coast Bloc

Distribution. – Eastern part of Côte d'Ivoire from V-baole eastwards to Volta river in eastern Ghana.

Knowledge. – Rather well explored (SCHIØTZ, 1967).

Description. – Forest much degraded and fragmented.

Endemics. – *Hyperolius bobirensis*; *H. laurenti*; *H. viridigulosus*. The latter occurs also in the easternmost part of block 1, east of river Sassandra.

Block 3. TransVolta-Togo

Distribution. – A narrow peninsula of forest-clad hills and low mountains in Ghana east of Volta river and in western Togo.

Knowledge. – Not well explored (SCHIØTZ, 1967, RÖDEL & AGYEI, 2003).

Endemics. – Two endemic treefrogs, the parasylvicolous *Hyperolius baumanni* and the sylvicolous *H. torrentis*.

Block 4. Southern Nigeria

Distribution. – From the Dahomey Gap (or Benin Gap) to Cross river.

Knowledge. – The parasylvicolous fauna is well explored, the sylvicolous fauna that may exist in the few and scattered remaining forests is almost unexplored (SCHIØTZ, 1967).

Description. – Southern Nigeria from the border with Benin to Cross river is today a forest-savanna mosaic so heavily influenced by man that closed-canopy forests are few and scattered. These forests have not been the subject of qualified collection, so the sylvicolous fauna, if still existing, is almost unknown. Collections indicate one, possibly two sylvicolous species belonging to western blocks (*Afrixalus nigeriensis*; possibly *Leptopelis occidentalis*), a few to the eastern (*Ophistothylax immaculatus*; *Leptopelis brevirostris*, possibly *L. boulengeri*).

Block 5. Cross-Sanaga Coastal Forests

Distribution. – From Cross river in eastern Nigeria to Sanaga river in Cameroun, covering the coastal lowlands and the forested parts of the Cameronese ridge.

Knowledge. – Very well explored (PERRET, 1966; AMIET, 1986). Unpublished fauna list distributed privately by Amiet in 2004 (AMIET, pers. comm.).

Description. – The lowlands are today a mosaic of humid forest, degraded forest and farmland. Mount Cameroun and the Cameronese ridge have a number of species often regarded as montane but, according to Amiet (in litt.), only *Afrixalus lacteus* is strictly so.

Endemics. – "Montane" species, endemic to the ridge, are: *Hyperolius riggenbachi* (found also at low altitude on the Benue plains), *Afrixalus lacteus* and some populations of *Leptopelis modestus*. In lowlands, *Arlequinus krebsi*, *Alexteroon jynx* and the enigmatic *Afrixalus schneideri*.

Block 6. Congolian Coastal Forests

Distribution. – Stretching from Sanaga river in Cameroun in a belt along the Atlantic coast to Angola. South of Cameroun, the vegetation is a mosaic of forests and savannas. The eastern limit towards block 7 is not well defined. The southern limit seems to coincide with the border Angola-République Démocratique du Congo although one, probably two parasylvicolous species, *Afrixalus dorsalis* and probably *Hyperolius adspersus*, are found as far south as coastal central Angola.

Knowledge. – Northern part (Cameroun) is very well explored (see under block 5). Scattered collections from further south: mount Alen, Equatorial Guinea (LASSO et al., 2002; RIVA, 1994), central Gabon (FRETEY et al., 1998, 2001), south-western Gabon (BURGER et al., 2004), south-western Republique du Congo (LARGEN & DOWSETT-LEMAIRE, 1991) and Mayombe, coastal République Démocratique du Congo (LAURENT, 1943, 1972, 1976, 1982).

Description. – The northern, well explored part (Cameroun) has one endemic species, *Hyperolius dintelmanni*, and shares the following with block 5: *H. acutirostris*, *H. bopeleti* and *Chlorolius koehleri*. *Hyperolius endjami* and *Leptopelis rufus* are endemic for block 5 and 6. In north-western Gabon, *Leptopelis crystallinoron* is found. Several species are common for block 5 and 6 and furthermore occurring to the east (table 2). Otherwise this region is characterised by the occurrence of a number of West African parasylvicolous species (p. 26). No sylvicolous species is known south of the border Angola-République Democratique du Congo.

Block 7. North-western Congolian Forests

Distribution. – Preliminary delimitation are Ubangi and Congo rivers and to the west the Congolian Coastal Forests.

Knowledge. – The part of the forested Congo cuvette situated in south-eastern Cameroun has been explored by Amiet but, according to him (in litt.), needs further research. The remaining area is virtually unexplored. The entire Congo basin (blocks 7, 8, 9, part of 6) has been covered by papers by LAURENT: *Hyperolius* (1943), *Leptopelis* (1972*b*), *Cryptothylax*, *Kassina* and *Phlyctimantis* (1976), *Afrixalus* (1982). Outside of the three old national parks these papers, however, are based on scattered and limited material. Of these parks only part of one, Parc National des Virunga, is within the scope of the present paper.

Endemics. – No endemic treefrogs are known for this block.

Note. – The Congo-Lualaba and Ubangi rivers are regarded by WWF (OLSON & DINERSTEIN 1998) as borders between ecoregions – here listed as 7, 8 and 9. It may seem doubtful if rivers in the wettest forest or swamp forest along them really are major zoogeographical borders for Amphibia.

Block 8. Central Congolian Forests

Distribution. – The forested parts of the Congo basin, south of the Congo-Lualaba river.

Knowledge. – The least known of the ecoregions. Only few, scattered collections (SCHIØTZ, 2006).

Endemics. *Cryptothylax minutus*, *Kassina mertensi*, *Hyperolius ghesquieri*, *H. robustus* and *H. sankuruensis* are recorded only from this region, but since they all are known only from a single or very few localities, their real distribution is unknown.

Block 9. North-eastern Congolian Forests

Distribution. East of Ubangi river, north and east of Congo-Lualaba river, here taken also to include forests at medium altitude in Uganda and westernmost Kenya. In WWF's Global 200 (Olson & Dinerstein, 1998), the eastern border is set at the Albertine rift.

Knowledge. Virunga National Parc (mainly savanna-forest mosaic) is well explored (Laurent, 1950, 1972*a*), but in spite of large collections the sylvicolous lowland fauna is virtually unknown. There are lowland collections mainly from the Ituri area (Noble, 1924, names updated by Poynton, 1998) and from montane western Uganda (Drewes & Vindum, 1994), and collections from forests at low and medium altitude in Uganda and western Kenya (Schiøtz, 1975; Schick et al., 2005). Otherwise very few collections exist. The suggested border areas between this block and blocks 7 and 8 are quite unexplored.

Endemics. From lowland, the imperfectly known *Hyperolius ferrugineus* and *H. langi* (appendix 3). *Afrixalus leucostictus* may also be endemic: one doubtful record exists from block 8 (Laurent, 1982), this specimen has been examined, and I find it impossible to decide whether it is *A. equatorialis* or *A. leucostictus*. Endemic are also the parasylvicolous *Leptopelis fiziensis*, *L. mackayi*, *Hyperolius lateralis* and *H. hutsebauti*.

The Albertine Rift mountains and highlands harbour a number of montane forest-related treefrogs, all endemic to these mountains, several of them very poorly known and with no ecological information: *Callixalus pictus*, *Hyperolius frontalis*, *H. alticola*, *H. castaneus*, **H. chrysogaster*, **H. diaphanus*, *H. leleupi*, **H. leucotaenius*, **H. xenorhinus*, **Leptopelis fenestratus* and *L. kivuensis*. Those with an * are omitted in this study because of lack of information about habitat.

Block 10. Eastern Forests

Distribution. The forest block, as here understood, consists of small patches of moist, closed-canopy forests in eastern Tanzania and Malawi (Eastern Arc mountains and outlying mountain blocks to the south) with a mixture of sylvicolous and parasylvicolous species, and of areas of dry, semi-deciduous forests in the lowland to the east and south-east of the Eastern Arc with a mixture of parasylvicolous and savanicolous species. The dry forests form a mosaic with Miombo Woodland from coastal Kenya to north-eastern South Africa. This latter area has been termed eastern lowlands (Schiøtz, 1976; Poynton, 1995, 1999). The southern border of this block is here set at approximately 22°S, which seems to represent the southern limit of the parasylvicolous tropical fauna of treefrogs (*Leptopelis flavomaculatus*, *Hyperolius puncticulatus* and *H. mitchelli*). Other parasylvicolous species occurring further south, in South Africa, are not treated in this study.

The eastern forests are separated from the forests in Central and West Africa by an impressive gap of dry savanna, approximately 500 km wide or more, termed "the arid corridor" by Poynton (1995).

Knowledge. – Well explored (SCHIØTZ, 1975, POYNTON, 2000*b*).

Endemics. – The entire sylvicolous and parasylvicolous fauna in this block is endemic.

Description. – It is important to note that the large forest block "Eastern Forests" as here understood differs profoundly from the other forest blocks: whereas these other blocks have closed canopy forest ("rainforest") as their climax vegetation and have been almost totally forest clad until the influence of man, the climax vegetation in the eastern forests outside of the Eastern Arc is either dry, semi-deciduous forest or forest-savanna mosaic. Only on the Eastern Arc and a few areas to the south of them is the climax vegetation moist evergreen forest with a sylvicolous fauna. The distinction between forest types versus the distinction between a montane and a lowland fauna is discussed on p. 19.

DISCUSSION

Tables 1 and 2 summarize the distribution along transect lines (fig. 2), subdivided in table 2 as in fig. 8.

The sylvicolous fauna shows a complete separation at species level between the three major regions with the Dahomey Gap or southern Nigeria as one divide, the Arid Corridor as the other. These regions are thus: (1) West Africa west of the Dahomey Gap; (2) Central Africa from southern Nigeria eastwards, (3) the forests of the Eastern Arc mountains. These regions can be subdivided into a number of forest blocks as indicated above (fig. 1).

The West African forest blocks 1 to 3 are reasonably well explored, well defined and well delimited. They differ most conspicuously in the genus *Hyperolius* for which each block has its distinct fauna of sylvicolous species. Three of the endemic species in block 1 are only known from the central part of the block, western Côte d'Ivoire (*Kassina lamottei*, *Hyperolius wermuthi* and *H. nienokouensis*). This central part of the block is the best investigated, which might explain why these secretive species were found there, or the species may be confined to the wettest, central part of the block, as suggested by RÖDEL (in litt.)

The blocks west of the Dahomey Gap (blocks 1-3) are completely separate at species level from block 5 and eastwards, but the badly explored – and much degraded – southern Nigeria (block 4) seems to represent a transition, with the occurrence of the western *Afrixalus nigeriensis* and the eastern *Opisthothylax immaculatus* and *L. brevirostris*. Either the western *L. occidentalis* or the eastern *L. boulengeri* were collected there (SCHIØTZ, 1967)

Blocks 5 and 6 have today a confluent forest cover, but with signs (patches of savanna) of having formerly been divided by a savanna tongue along the Sanaga river (AMIET, 1987). In a study of some typical Cameronese amphibia – not including any treefrogs –, AMIET (1987) has demonstrated the importance of the Sanaga river as a border between several species or subspecies pairs, such as *Leptodactylodon a. albiventris* versus *L. a. bueanus*, *Leptodactylodon ovatus* vs. *L. ventrimarmoratus*, *Astylosternus diadematus* vs. *A. batesi*, and *Cardioglossa nigromaculata* vs. *C. gratiosa*. In general the difference in the treefrog fauna in Cameroun north and south of the Sanaga river is not conspicuous (AMIET, in litt.). *Arlequinus krebsi* and *Alexteroon jynx* are endemic to the northern block, *Hyperolius mosaicus* occurs only south of the river whereas *Hyperolius acutirostris* and *H. endjami* are common to block 5 and the northern, Cameronese part of block 6. *Leptopelis rufus* seems endemic to the entire blocks 5 and 6.

The fauna of block 6 is not very distinct. Almost all the sylvicolous treefrogs known from this block are found also in block 5 to the north and/or in blocks 7-8 further east (table 2). The part of block 6 situated south of the Cameronese border seems poorer in species (both sylvicolous and parasylvicolous) than the Cameronese part of block 6. It cannot be said whether this is due to the fauna becoming poorer south of Cameroun – as is the case when moving from Cameroun to the west – or because there has been far less collecting effort in this area.

Block 7, south-eastern Cameroun and north-western Congo, has no sylvicolous species distinct from block 6. This is probably not due to lack of collecting, for although much of region 7 is virtually unexplored, its north-western corner (south-eastern Cameroun) is well explored. Of block 7, only the north-western corner, in Cameroun, is explored, of block 9 only the north eastern, leaving a virtually unexplored gap of more than 1000 km, and we completely lack collections showing whether the suggested borders between the blocks – or ecoregions in WWF's terms – 7, 8 and 9 (Congo and Ubangi rivers) are well-defined faunal breaks, or whether the fauna changes gradually.

Block 8 is the least explored of the recognized blocks, since only scattered, rather unsystematic collections have been made. Attempt by the author to collect in this block in 1975 and 2005 met only with limited success and could confirm an impression of a species-poor fauna. The five apparent endemic species for this region are so badly known that nothing can be said of their real distribution.

Block 9 has apparently only one endemic sylvicolous lowland species (*Afrixalus leucostictus* albeit with one doubtful locality in block 8), in addition to a number of species confined to highlands at the Albertine rift. In the lowlands outside these mountains the numbers of sylvicolous species are low (5) which seems difficult to explain except as a collection artefact, remarkable in view of the large collections made in Parc National des Virunga, also in its low-lying, partly forested parts (Laurent, 1950, 1972). Large collections by non-specialists do, however, not necessarily mean that all species are ultimately found. Only 3 sylvicolous *Leptopelis* and no sylvicolous lowland *Hyperolius* reported from this area would point towards grave under-collecting.

Forest block 10, Eastern Forests, has a fauna, both sylvicolous and parasylvicolous, completely separate at species level from the fauna of the remaining blocks. The sylvicolous fauna is almost exclusively found in the forests of the Eastern Arc where local topography has ensured sufficient rainfall to maintain a closed canopy forest also through drier periods. Considering the minute size of these forests, probably also in the past, the fauna is quite rich. The forests are today split into a number of isolated units the best explored of which are eastern Usambara, western Usambara, Uluguru and Udzungwa. The distribution pattern between these isolated forest "islands" seems very similar to the pattern of the two major West African regions, 1 and 2, namely that the genera *Leptopelis* and *Afrixalus* have species in common for these "islands", whereas the two known sylvicolous *Hyperolius* seem endemic to one of the islands. The distributions of these sylvicolous *Hyperolius* are, however, not well known – both species are only known from the type locality – and they may be more widely distributed, so no attempt was made to divide the Eastern Arc Forests into separate forest blocks on this slender evidence. The dry forests in the lowlands, including the coastal forests, harbour a parasylvicolous fauna (p. 26).

The fauna and flora in the Eastern Arc Forests is conventionally termed a montane fauna and flora (e.g., LOVETT, 1988, 1990; POYNTON, 1990, 1999, 2000, POYNTON et al., 2006) as different from the lowland fauna, the forest-related fauna in the eastern lowlands. I have in the present study preferred to distinguish between a sylvicolous and a parasylvicolous fauna rather than between a montane versus lowland fauna. Although we do not know the causal connections between altitude and/or vegetation and the distribution of animals, I do find such a distinction more relevant for a study of the treefrogs since the known altitudinal ranges (app. 4) do not seem to support a distinction based on altitude. The sylvicolous fauna is found as far down as the closed canopy forest (to 200 m on eastern slopes of the Usambaras), whereas the parasylvicolous fauna is found as far up as the right habitat (degraded forest and farmland) is found in the Eastern Arc mountains as well as in dry forest in the lowland. The closed canopy forest seems to harbour the sylvicolous fauna of treefrogs regardless of its altitude, and the degraded forests harbour the parasylvicolous fauna regardless of its altitude. Some species (*Hyperolius tannerorum*, *H. kihangensis* and *Phlyctimantis keithae*) were only recorded from localities higher than 1400 m, but since they are only known from one or a few localities it is unclear whether they are confined to such altitude. I do not see a dramatic deviation from common thinking by viewing the distribution of the treefrogs from a sylvicolous/parasylvicolous perspective rather that one determined by altitude, remembering Hengeveld's dictum, cited in POYNTON & BROADLEY (1991): "[biogeographical] classifications are not right or wrong, only useful or not".

The general picture for the sylvicolous treefrogs in tropical Africa is that the genus *Hyperolius* shows the maximal species diversification (fig. 3) with distinct species in each forest block. This is clearly the case in Western Africa and along the Atlantic Coast (blocks 1-5 and the northern part of 6), whereas the data for Central Africa (blocks 7-9) are far too incomplete to draw any conclusion. In fact, the only sylvicolous *Hyperolius* we know from these regions are known from single localities. In the well-explored Eastern Forests, the only known sylvicolous *Hyperolius*, *H. tannerorum* and *H. kihangensis*, seem to be confined to one forest each (western Usambaras and Udzungwas), although they may have been overlooked elsewhere.

Hyperolius ocellatus seems to be the only sylvicolous *Hyperolius* breaking this pattern, being found in blocks 5, 6, 7, 8 and 9. It may be significant that this is a species being both sylvicolous and parasylvicolous (AMIET, 1986, in litt.), although predominantly sylvicolous.

The genera *Leptopelis* and *Afrixalus* are more widely distributed (fig. 4), in most cases so that one set of species is found in West Africa (block 1-3), another in Central Africa (5-9) and yet another in the Eastern Forests. *Alexteroon* may belong to this group, although the distribution of its three members outside of Cameroun is badly known.

Finally, there is a group of sylvicolous amphibia with a wide distribution in blocks 1 to 9, namely, with our present understanding of their taxonomy, some *Bufo* and *Ptychadena*, and the only sylvicolous rhacophorid, *Chiromantis rufescens*. No sylvicolous Hyperoliidae or *Leptopelis* has such a wide distribution (fig. 5).

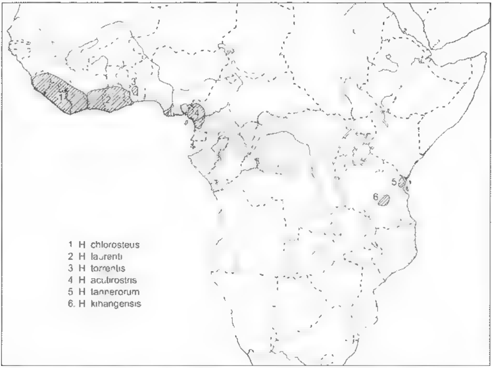


Fig. 3. — Maximal species diversification in sylvicolous Amphibia. This pattern is shown by sylvicolous *Hyperolius*. Our knowledge of the sylvicolous *Hyperolius* in the Congo basin is not sufficient to indicate distribution here.

The genus *Kassina* has only one sylvicolous member, *K. lamottei* from western Côte d'Ivoire, *Phlyctimantis* and *Cryptothylax* none. The genus *Acanthixalus* is so cumbersome to collect that little can be said about its real distribution. One species is known from two localities in West Africa, the other species from a few widely scattered localities in Central Africa. *Opisthothylax* consists of one sylvicolous species in Central Africa.

An attempt is made to make a hierarchical dendrogram illustrating the similarity between the sylvicolous treefrog faunas in the forest blocks (fig. 6) through the Quotient of Similarity (QS) (p. 7). The QS should in the present case be taken with great reservation since several blocks are badly explored and/or the number of taxa is so low that the discovery of a single or a few taxa may change its value considerably. Therefore blocks 3 and 4 have been omitted and 7, 8 and 9 combined. Block 10 has been divided into three units, Usambaras (10a), Ulugurus (10b) and Udzungwas (10c). The difference between these reflects the occurrence of the two sylvicolous *Hyperolius*, which may or may not be endemic to Usambaras and Udzungwas respectively. An attempt is also made to show similarity between block 5 and those parts of blocks 6 and 7 situated within the well-explored Cameroun in order to analyse similarities between areas with comparable exploration.

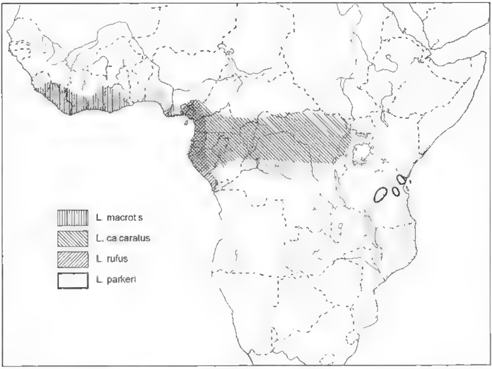


Fig 4 Medium species diversification in sylvicolous Amphibia This pattern is shown by sylvicolous *Leptopelis* and *Afrixalus*

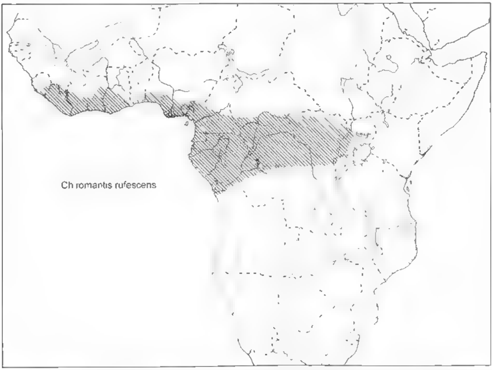
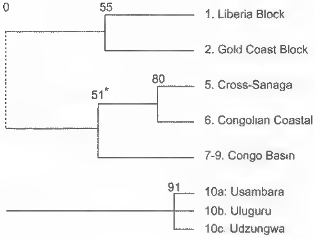


Fig 5 Minimal species diversification in forest Amphibia This pattern is not shown by any Hyperolidae or *Leptopelis*

Source - MNHN, Paris



	5	6n	7nw
5	-	82	64
6n		-	53

	10a	10b	10c
10a	-	91	83
10b		-	91

Fig. 6. – Quotient of Similarity between sylvicolous Amphibia in forest blocks. See text for explanation. *, QS between 5+6 versus 7-9.
The two tables show in greater details the QS between selected areas.

There are no common taxa between the three "ecoregions", blocks 1-2, 5-9 and 10. When a possible connection between 1-2 and 5-9 nevertheless is indicated in fig. 6, is it because it could be argued that these regions show similarity in their faunas through species pairs, probably closely related. The West African *Leptopelis macrotis*, *L. occidentalis*, *Afrixalus vibekensis* and *Acanthixalus sonjae* may thus have "sister species" in Central Africa, namely *L. rufus* or *L. millsoni*, *L. boulengeri*, *Afrixalus laevis* and *Acanthixalus spinosus*. An additional argument is also that several members of other families, such as *Chiromantis rufescens*, several *Bufo*, etc., are in common between these ecoregions. Block 10 has only one species, *Afrixalus uluguruensis* showing similarity to a Central African form, *A. laevis*. The four *Leptopelis* seem dissimilar to any of their Central African counterparts. It can therefore be argued that the sylvicolous fauna of West and Central Africa may have a common root, whereas the fauna of the Eastern Arc Forests has developed independently of the rest of Africa's forest treefrogs.

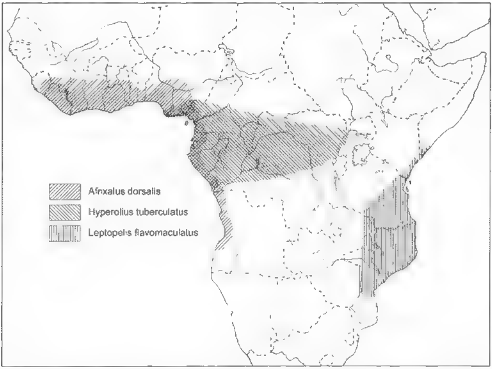


Fig. 7 The three typical distribution patterns found among the parasylvicolous treefrogs: a West African distribution (*Afrixalus dorsalis*, the species which is found further to the South), a Central African distribution (*Hyperolius tuberculatus*) and an East African distribution (*Leptopelis flavomaculatus*)

THE PARASYLVICOLOUS FAUNA

DISTRIBUTION

The distribution of the parasylvicolous fauna shows a pattern fundamentally different from that of the sylvicolous fauna. The overall picture is of three separate regions where, however, the borders between two of them differ from those of the sylvicolous faunas (fig. 7):

(1) A western fauna found throughout West Africa and further south in a belt along the Atlantic coast of Central Africa (blocks 5 and 6). *Afrixalus dorsalis* and probably *Hyperolius adspersus* are found as far south as coastal central Angola, the other species taper out farther north along the coast (table 3 and fig. 8). It is noteworthy that none of these West African species are found further inland in Central Africa into block 7, in spite of lack of obvious physical or vegetation barriers.

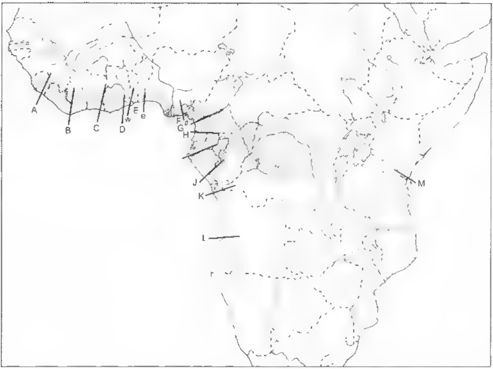


Fig 8. – Boundaries in the distribution of parasylvicolous treefrogs.

The lines A-G are based on a dense network of collecting localities and in most cases on the occurrence of vicariant taxa on either side of the line. In contrast, the credibility of the boundaries H-K is basically different since collecting there was so sporadic that arbitrary lines had to be drawn based on the scattered collections, and placed roughly between such collecting localities and between the refuges proposed in fig. 9. Available data do not permit to conclude that the boundaries between several pairs of vicariant taxa coincide exactly, even when this map implies so.

A, Eastern limit for *Hyperolius occidentalis*, and western limit for *H. picturatus*, *H. concolor* and *Afrixalus d. dorsalis*

B, Boundary *H. f. fusciventris* vs. *H. f. lamtoensis*, and *Kassina cochranae* vs. *K. arboricola*

C, Eastern limit for *H. f. burtoni*, and boundary *H. sylvaticus ivorensis* vs. *H. s. sylvaticus*

D, Boundary *H. picturatus* vs. *H. baumanni*

E, Dahomey Gap, where w and e represent the western and eastern border of the savanna gap boundary *H. s. sylvaticus* vs. *H. s. nigeriensis*, *H. c. concolor* vs. *H. c. ibadanensis*, and eastern boundary for *K. arboricola*

F, Cross river: boundary *H. c. ibadanensis* vs. *H. c.* ssp., *L. hyloides* vs. *L. aubryi*, *H. f. burtoni* vs. *H. f.* ssp., and western limit for *H. bolifambae*, *H. ocellatus*, *A. paradorsalis* and *H. kuligae*

G, Sanaga river: southern limit for *H. fusciventris*, *H. sylvaticus* and *H. concolor*, north-western limit for *H. pardalis*, *H. platyceps* and *H. phantasticus*, northern limit for *Cryptothylax greshoffii* and south-eastern limit for *H. camerunensis*.

H, Boundary Cameroun-Rio Muni: boundary *A. d. dorsalis* vs. *A. d. regularis*, and *Phlyctimantis leonardi* vs. *P. boulengeri*.

I, Central Gabon

J, Boundary Gabon-République du Congo: southern limit for *H. guttulatus*, *L. notatus* and *H. pardalis*.

K, Boundary République Démocratique du Congo-Angola: southern known limit for *L. aubryi*, *H. phantasticus*, *H. adspersus* (?), *P. leonardi* and *C. greshoffii*, northern limit for *A. osorioi* along coast.

L, Southern limit for *A. dorsalis regularis* and probably *H. adspersus*

M, Boundary *H. mitchelli* vs *H. rubrovermiculatus*

(2) A Central African fauna, from Cross river eastwards, different from the western fauna at species level. In the western part of the range, in the Cross-Sanaga forest and Congolian Coastal Forest ecosystem, this fauna is overlapping with the western fauna

(3) A distinct fauna in the Eastern Forests showing a total separation at species level from the remaining forests.

There is a considerable splitting up into subspecies, especially in the western fauna.

DISCUSSION

A pattern similar to the splitting up of the sylvicolous Hyperoliidae into distinct insular faunas in discrete forest blocks is not seen among the parasylvicolous species. Instead, there is a considerable splitting up at places that appear "random" in the way that a clustering in groups of taxa sharing the same distribution seems to be lacking (fig. 8). This is especially apparent in the well-explored West Africa-Cameroun region and at the subspecific level in the most "versatile" genus, *Hyperolius*. In SCHIØTZ (1967), this "random" splitting up in West Africa was explained by the natural habitat, namely open, dry forest, being originally only found in a narrow belt, a forest edge at the well-defined forest-savanna border - plus in gallery forests stretching as tongues up into the savanna. Only when man disrupted the moist forest belt through farming and felling and thus created a network of open habitats, did large areas become suitable for the parasylvicolous fauna. Such an original, "linear" or "one-dimensional" distribution might facilitate taxonomic splitting up at rather insignificant and perhaps temporary barriers.

The westernmost part of West Africa (western Sierra Leone and adjacent parts of Guinea and Senegal) seems distinguished by the presence of the endemic *Hyperolius occidentalis*, as well as by the absence of the otherwise abundant and widespread species *Hyperolius concolor*, *H. picturatus* and *Afrixalus dorsalis*.

It is noteworthy that the two most distinct gaps for the sylvicolous faunas in West Africa are either not recognisable for the parasylvicolous fauna (V-baole) or rather unimportant (Dahomey Gap).

The Cross river is the western limit for several central African species, whereas a majority of the parasylvicolous species from West Africa continues along the Atlantic coast at least into Cameroun. The parasylvicolous fauna of the Cross-Sanaga and the Congolian Coastal Forests thus consists of two distinct fauna elements, a Central African mixed with a distinct West African element where no less than 5 out of the 8 parasylvicolous species of treefrogs occurring in Ghana are also found in remote Cameroun, including 4 out of 5 *Hyperolius*, a number tapering out when moving south from Cameroun along the coast. None of them are found inland in Central Africa. In comparison, none of the sylvicolous treefrogs from Ghana occurs in Cameroun.

Another element of parasylvicolous species is widely distributed in the Congo Basin but a closer analysis of the parasylvicolous fauna of central Africa is not possible with our present knowledge.

The Eastern Forest has a pattern of distribution different from the western forest blocks. The parasylvicolous fauna is widely distributed on suitable localities in the eastern lowlands as well as on the Eastern Arc. Contrary to the proposed "linear" or "one-dimensional" original distribution in West Africa, the original (i.e., before man transformed the landscapes) distribution of the parasylvicolous species in the eastern forest has been "two-dimensional", not confined to a narrow zone between moist forest and savanna, since the climax vegetation in the eastern forests has been large areas with a dry forest/savanna mosaic, habitable throughout by the parasylvicolous fauna. Of the parasylvicolous species in the eastern forests, only the species pair *Hyperolius mitchelli* vs. *H. rubrovermiculatus* (found respectively south and north of the Kenya-Tanzanian border) shows a pattern similar to that of West Africa with vicariant taxa replacing each other. Significantly this is where this eastern forest becomes a narrow "corridor" near its northern border, and a division there could be explained in the same way as the distribution pattern in West Africa (fig. 8).

Poynton (1990) discussed the distinctness of the East African lowland fauna (below 300 m) and reached the conclusion that this fauna is not well defined or well delimited, but that nevertheless the lowland fauna has "a homogeneity which accords with the idea of a discrete 'fauna'" (p. 291). If his analysis (e.g., his figure 4) had included all the parasylvicolous frogs and had separated them from the savanicolous group, a much clearer pattern would have emerged with a distinct fauna found in the eastern lowlands, but generally penetrating higher up than the 300 m limit, into the parasylvicolous habitats in the Eastern Arc forests, apparently as high up as such habitats are found or explored (app. 4). Members of this fauna are here found to above 1000 m, sympatric with the sylvicolous fauna. West of the Eastern Arc mountains, the parasylvicolous fauna of block 10 seems to be absent, perhaps because of absence of the relevant habitats throughout the Arid Corridor.

Poynton (1999: 485) found "endemism relatively low" in the East African lowlands. I claim, however, that endemism in the forest block here termed eastern forests is 100 %, not only for treefrogs, but also for other Amphibia. This apparently dramatic discrepancy is partly because Poynton limited his study to lowlands below 300 m, although a significant part of the fauna is found higher up, partly because I restrict my study to the parasylvicolous and sylvicolous faunas, omitting the numerous savanicolous species, many of which are found further inland.

The montane faunas

Several families of Anura have a strong element of orophile, forest-related species and genera. In many cases the tadpoles are adapted to swift-flowing streams, and the species could be termed rheophile rather than orophile. No rheophile treefrogs are known, and an orophile element in this group is ill-defined and seems weak. A number of species are only or predominantly found above 1000-1500 m and are often regarded as montane, but it can be argued that there are few real montane species among the treefrogs since most species can be found as far down as suitable vegetation is found, to 100-200 m. Therefore no attempt has been made to distinguish the montane species as a special category in this study.

The "montane" species in the tropical forest belt are found in three areas, namely mount Cameroun and the Cameronese ridge, the Albertine rift mountains including the Itombwe plateau, and finally the Eastern Arc mountains. The "montane" treefrog faunas in these three areas are separate from each other at species level. The best developed orophile element is found in the Albertine rift montane areas with a number of species known only from high altitude (see block 9, p. 16). In the Eastern Arc mountains, a few species are known only from altitude above 1000 m but they are all species known from so few localities that a realistic assessment of their altitudinal distribution is uncertain (app. 4, discussion p. 19). In the Cameronese ridge only one treefrog, *Afrixalus lacteus*, is confined to high altitude, the remaining treefrogs from this area can occasionally be found at low altitude (AMIET, in litt.). The well-investigated mount Nimba (1750 m) in West Africa has no orophile treefrogs.

CONCLUSION

THE HISTORY OF THE SYLVICOLOUS AND PARASYLVICOLOUS FAUNAS

In SCHIØTZ (1967), it was postulated that the distribution pattern of the West African sylvicolous treefrogs could be explained fully from the vicissitudes in late Pleistocene, during which the last arid period has divided the forest into isolated islands for sufficiently long periods to allow the most versatile genus, *Hyperolius*, to develop discrete species, while the more conservative genera *Afrixalus* and *Leptopelis* did not show a splitting up on either side of V-baole, but a distinct break at the species level at the Dahomey Gap. The most conservative genera *Chiromantis*, *Bufo* and *Ptychadena* show only limited division between West Africa and Central Africa. There are thus three "levels" of species diversification for the sylvicole Amphibia (fig. 3-5)

The relevant factors seem to be climatic fluctuations resulting in vegetational fluctuations during the latter part of Pleistocene, over approximately the last 40,000 years (TINSLEY et al., 1996, MALEY, 1996): a cold and arid period from 40,000 to 12,000 years before present (ybp) resulted in the lowland forest retracting considerably, to be partly replaced by savanna. Most extreme aridity occurred from about 25,000 to about 12,000 ybp, during the glacial maxima in the northern hemisphere. There is, however, extensive evidence that lowland rainforest persisted in a number of refugia determined by local conditions of altitude, precipitation and soil type. The most common state in the upper Pleistocene would be a relatively fragmented forest mass, but with larger areas of forest than those postulated for the most arid phase.

The end of the last glaciation was characterised by a rapid rise in temperature approximately 12,000 years ago. The lowland tropical forest expanded, reaching a maximum circa 7,000 ybp, a maximum which, however, did not unite the Central African forests with those of the Eastern Arc.

It is suggested (MALEY, 1996) that in the last major arid phase (circa 18 000 ybp) forest refugia persisted as two or three areas in West Africa, one in the Cross-Sanaga forest, four refugia in the Congolian Coastal forest, one large refugium along Congo river, another along the Albertine rift and finally a number of small refugia in the Eastern Arc mountains (fig. 9). COLYN et al. (1991) suggested a more complicated pattern for the Congo Basin.

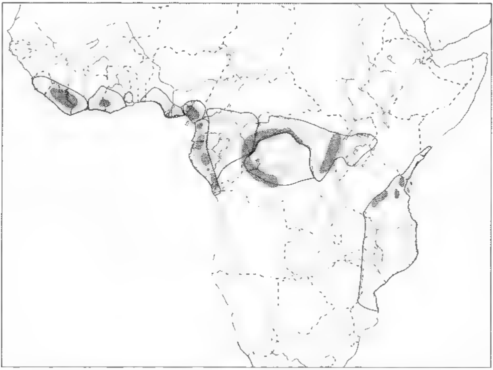


Fig. 9. – Proposed dry-period forest refugia. Redrawn after MALEY (1996), with a small refugium added at mount Doudou, Gabon, as proposed by SOSEF (1994). Also added are the Eastern Forests.

Based on the proposed forest refugia, one can explain the distinctness of blocks 1 and 2, and 5 and the northern part of 6, whereas the southern part of 6, south of Cameroun, and of 7, 8 and 9 are not well collected enough to allow drawing conclusions. Therefore the four or five refugia suggested (MALEY, 1996) from Equatorial Guinea (Rio Muni) to Mayombe cannot with our present knowledge be substantiated through the distribution of the treefrogs, although we have collections from localities situated at or very close to all of them.

The three ecoregions in the Congo Basin seem, with our present knowledge, to have a very similar lowland fauna. Whether the small differences between the three blocks point at three discrete regions with the Congo and Ubangi rivers as borders, or gradual changes in the huge Congo basin is not known. Three well-defined regions with clear borders, as suggested by WWF's divisions into ecoregions, would seem unlikely since drier periods in Pleistocene probably never split the Congo Basin forest up into three refugia separated by the river; a situation of Congo basin refugia as indicated in fig. 9 would seem rather more likely.

Data for primates supported by plants (COLYN et al., 1991) seem to point at faunal breaks in the Congo basin originating from several nuclear areas on both sides of the Congo-Lualaba river, suggesting that, during the last arid period, populations survived in several refugia within the Congo basin. Zones of intergradation strongly suggest that dispersal operated from these areas and not only from the Albertine rift and from the West Central (Cameroun-Gabon) refugia.

Block 10 shows no sign of having been connected with the rest of the blocks, with no species in common.

It is difficult to say whether the occurrence of several small genera of Hyperoliidae in Cameroun is caused by a refugium there having persisted even longer back in time, or by the forests there having been consistently wetter and thus more favourable for frogs and their diversification, or on the perseverance of herpetological scrutiny.

The forest in the Congo basin is frequently described in the literature as species-poor, a poverty explained by it being a young forest as shown by it standing on Kalahari sand. Thus FAIRBRIDGE (1968) wrote: "almost the whole Congo basin was invaded by dune sands from the Kalahari during the period 50 000-10.000 B.P", and many other authors supported this idea. WHITE (1993) rejected this theory and suggested it was based on confusion between "Kalahari sands" and the "Kalahari geological system" According to White, the sand dunes and formations are nowhere approaching the equator, and the forest in the central Congo basin is not particularly young

The theory that refugia in the lowland forests has acted as evolutionary centres was challenged by FJELDSÅ & LOVETT (1997) Based on birds and some plant families in forest biota, where the authors distinguished between old and young species, they did not find strong evidence for the importance of Pleistocene refugia as centres for allopatric speciation They saw the refugia rather as "museums", maintaining old species, and demonstrated that "the proliferation of young species takes place mainly at the periphery of the main rainforest blocks" The data for sylvicolous treefrogs, meagre when they are compared to birds and plants, might add arguments to this discussion. For most genera of Amphibia among the treefrogs *Leptopelis* and *Afrixalus* the refugia can be seen as museums, carrying sets of species through periods of forest division, but for *Hyperolius* the rule seems to be that each major, well-investigated forest block which has harboured a refugium has developed its own set of sylvicolous *Hyperolius* An explanation could be that the genus *Hyperolius* is more "versatile" so that the rather brief periods of isolation of the refugia have been sufficient for these refugia to act as evolutionary centres. *Hyperolius* would thus according to Fjeldså & Lovett's term be composed of "young species" The considerable subspecific splitting up of the parasylvicolous treefrogs compared to the sylvicolous may suggest the parasylvicolous taxa to be younger than the sylvicolous. The diversification of the parasylvicolous species, apparently unrelated to former forest refugia, seems to have taken place at "the periphery of the forest belt", namely along the original forest-savanna border (present paper, p. 15) Data for diversity of treefrogs (SCHIOTZ, 1999, fig 2) using WorldMap as basis for analysis, apparently support the view of Fjeldså & Lovett by showing a peak of diversity in the periphery of the forest belt, most conspicuous in the well-investigated West Africa A closer analysis of the data for treefrogs shows, however, that this is solely caused by an increased habitat diversity in the forest-savanna transition zone within the rather coarse 110 × 110 km grids used by WorldMap, where the sylvicolous, parasylvicolous and savanicolous faunas are superimposed None of these three faunas becomes more diverse here, understood as richer in species or subspecies, but all three faunas are present within a grid, as different from the condition further away from the transition zone. This comment is not relevant to Fjeldså & Lovett's own conclusions since they deal only with forest-related species.

In strong contrast to the explanation presented here of the present distribution pattern being explicable by climate fluctuations in late Pleistocene and *Hyperolius* being a genus of young species, Wieczorek et al. (2000) postulated a far longer history for the diversification in the genus *Hyperolius*. Their thesis is based on mtDNA sequence data, habitat preference and current distribution. By referring each node in their dendrogram, based on mtDNA (p. 1237), to a distinct geological, climatic and vegetation change – without making it clear why each step on their dendrogram necessarily corresponds with one step on their list of palaeoenvironmental changes – they claim that they can trace the species diversification in the genus *Hyperolius* back to Cretaceous and Palaeocene. An assessment of their theory is difficult since both their distribution maps and their references to habitat preference are unconventional. The authors thus work with habitat preferences savanna, forest and generalists. The latter term is not explained. If the term generalist refers to what is here termed parasylvicolous I do question the correctness. The parasylvicolous fauna does not seem more generalised in its habitat choice than the sylvicolous and savanicolous, and the 6 species referred to that category in their paper do not clarify matters since it refers to 2 montane sylvicolous species, 2 parasylvicolous and 2 savanicolous, whereas all their "forest species" are parasylvicolous in my terminology. Rather than giving distribution maps based on collected specimens, their distribution is "extrapolated taking into account... habitat utilisation". But since their allocation to habitat utilisation is most unconventional – and unexplained in the text – so are the resulting distribution maps.

A theory of theirs is that the genus *Hyperolius* originated as generalists and became increasingly specialised in terms of habitat. Strangely their only supporting argument, *Hyperolius cinnamomeoventris*, which is both the basal lineage on the dendrogram and the only suspected generalist in the genus (apparently being both parasylvicolous and savanicolous, unless it is a composite of several species), is termed in their paper as a forest species and would thus seem to contradict their thesis. Unfortunately no sylvicolous species from lowland forests is included in their study. Bringing species diversification in *Hyperolius* back to Cretaceous would make this genus the oldest African frog genus together with *Xenopus*. Not until Miocene do we have records of other families than Pipidae (Duellman, 1993). The latest diversification in their dendrogram on p. 1237 is during "Pleiocene" (Pliocene or Pleistocene?) but seems only to have influenced speciation in the superspecies *Hyperolius viridiflavus*, a group of very closely related savanicolous taxa.

I doubt whether the present species structure in *Hyperolius* has its rooting back in Cretaceous, 70 million years ago. I feel that *Hyperolius* shows many signs of being a very new genus, more in the process of rapid, recent speciation than most or all other African genera of Amphibia. I feel that the species pattern in the genus *Hyperolius* can be fully explained as the result of climatic and vegetation changes during late Pleistocene, a period of approximately 35,000 years.

ACKNOWLEDGEMENTS

The Carlsberg Foundation has through half a century generously supported my African fieldwork, the necessary basis for the present study, and has more specifically covered the cost of the publication of the present paper.

My colleagues J.-L. Amiet and J. C. Poynton as well as three reviewers, among them M.-O. Rödel, are thanked for their critical and constructive comments. Birgitte Rubæk, Zoological Museum in Copenhagen, has kindly produced the maps. J. C. Poynton and Anne Marie Warfield have revised the language at two stages of the manuscript.

REFERENCES

AMIET, J.-L., 1986. – La batrachofaune sylvicole d'un secteur forestier du Cameroun: la region de Yaoundé. *Mém. Mus. nat. Hist. nat.*, (A), **132**: 29-42.

----- 1987. – Aires disjointes et taxons vicariants chez les Anoures du Cameroun: implications paléoclimatiques. *Alytes*, **6** (3-4): 99-115.

----- 1989. – Quelques aspects de la biologie des Amphibiens Anoures du Cameroun. *Ann. biol.*, **28** (2): 73-136.

----- 2000. – Les *Alexteroon* du Cameroun. *Alytes*, **17** (3-4): 125-164.

----- 2001. – Un nouveau *Leptopelis* de la zone forestière camerounaise. *Alytes*, **19** (1): 29-44.

----- 2004*a*. – A propos de deux *Leptopelis* nouveaux pour la faune du Cameroun. *Alytes*, **21** (3-4): 111-170.

----- 2004*b*. – Une nouvelle espece d'*Hyperolius* du Cameroun. *Rev. suisse Zool.*, **111**: 567-583.

----- 2005. – Les *Hyperolius* camerounais du groupe d'*H. nasutus* (Amphibia, Anura, Hyperoliidae). *Rev. suisse Zool.*, **112**: 271-310.

BURGER, M., BRANCH, W. R. & CHANNING, A., 2004. – Amphibians and Reptiles of Monts Doudou, Gabon. *Calif. Acad. Sci. Mem.*, **28**: 145-186.

BURGER, M., PAUWELS, O. S. G., BRANCH, W. R., TOBI, E., YOGA, J.-A. & MIKOLO, E.-N., 2006. – An assessment of the amphibian fauna of the Gamba Complex of Protected Areas, Southwestern Gabon. *In*: A. ALONSO et al. (ed), *Gamba, Gabon: biodiversity of an African equatorial forest*, *Bull. biol. Soc. Washington*, **12**: 297-307.

COLYN, M., GAUTIER-HION, A. & VERHEYEN, W., 1991. – A re-appraisal of palaeoenvironmental history in Central Africa. *J. Biogeogr.*, **18**: 403-407.

DIAMOND, A. W. & HAMILTON, A. C., 1980. – The distribution of forest passerine birds and Quarternary climate changes in tropical Africa. *J. Zool.*, London, **191**: 379-402.

DREWES, R. C. & VINDUM, J. V., 1994. – Amphibians of the Impenetrable Forest, SW Uganda. *J. afr. Zool.*, **108**: 55-70.

DUBOIS, A., CROMBIE, R. I. & GLAW, F., 2005. – *Amphibia Mundi*. 1.2. Recent amphibians: generic and infrageneric taxonomic additions (1981-2002). *Alytes*, **23** (1-2): 25-69.

DUELLMAN, W. E., 1993. – Amphibians in Africa and South America: evolutionary history and ecological comparisons. *In*: P. GOLDBLATT (ed.), *Biological relationships between Africa and South America*, Yale, U.P.: 200-243.

FAIRBRIDGE, R. W., 1968. – Terraces, fluvial-environmental controls. *In*: R. W. FAIRBRIDGE (ed.), *Enclypedia of geomorphology*, **3**: 1124-1138.

FJELDSÅ, J. & LOVETT, J., 1997. – Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biol. Conserv.*, **6**: 325-346.

FRÉTEY, T. & BLANC, C. P., 2000. – Liste des Amphibiens d'Afrique centrale. *Dossiers de l'ADIE*, **2**: 1-40.

----- 2001. – Inventaire systématique des Amphibiens Anoures du centre du Gabon. *Bull. Soc. zool. France*, **126** (4): 375-390.

Fretey, T. & Dewynter M., 1998. – Amphibiens Anoures de la forêt des Abeilles (Gabon). *J. afr. Zool.*, **112** (3): 171-184.

Frost, D. R., Grant, T., Faivovich, J., Bazin, R. H., Haas, A., Haddad, C. F. B., de Sá, R. O., Channing, A., Wilkinson, M., Donnellan, S. C., Raxworthy, C. J., Campbell, J. A., Blotto, B. L., Moler, P., Drewes, R. C., Nussbaum, R. A., Lynch, J. D., Green, D. M. & Wheeler, W. C., 2006. – The amphibian tree of life. *Bull. amer. Mus. Nat. Hist.*, **297**: 1-370.

Guibé, J. & Lamotte, M., 1958. – Reserve naturelle du Mt Nimba, Batraciens. *Mem. IFAN*, **53**: 241-273.

Köhler, J., Bwong, B. A., Schick, S., Veith, M. & Lötters, S., 2006. – A new species of arboreal *Leptopelis* from the forests of western Kenya. *Herp. J.*, **16**: 183-189.

Largen, M. & Dowsett-Lemaire, F., 1991. – Amphibians from the Kouilou River Basin, Rép. du Congo. *Tauraco Research Rep.*, **41**: 45-168.

Lasso, C. A., Rial, A. I., Castroviejo, J. & Riva, I. de la, 2002. – Herpetofauna del Parque Nacional de Monte Alén, Rio Muni. *Graellsia*, **58** (2): 21-34.

Laurent, R. F., 1943. – Les *Hyperolius* du Musée du Congo. *Ann. Mus. Congo belge*, (1), **4**: 61-140.

----- 1950. – Genres *Afrixalus* et *Hyperolius*. *Expl. du Parc nat. Albert, Miss. de Witte*, **64**: 1-120.

----- 1958. – La reserve du Mt. Nimba. Les Rainettes du genre *Hyperolius*. *Mem. IFAN*, **53**: 275-299.

----- 1972*a*. – Amphibiens. *Expl. du Parc Nat. des Virunga*, **22**:1-125.

----- 1972*b*. – Le genre *Leptopelis* au Zaïre. *Ann. Mus. r. Afr. centrale*, **202**: 1-62.

----- 1976. – Les genres *Cryptothylax*, *Phlyctimantis* et *Kassina* au Zaïre. *Ann. Mus. r. Afr. centrale*, **213**: 1-67.

----- 1982. – Le genre *Afrixalus* en Afrique centrale. *Ann. Mus. r. Afr. centrale*, **235**: 1-58.

Lötters, S., Rödel, M.-O. & Burger, M., 2005. – A new large tree frog from north-western Gabon. *Herp. J.*, **15**: 149-152.

Lötters, S. & Schmitz, A., 2004. – A new species of tree frog from the Bakossi Mountains, south-west Cameroun. *Bonner zool. Beiträge*, **52**: 149-154.

Loveridge, A., 1937. – Scientific results of an expedition to rain forest regions in eastern Africa. IX. Zoogeography and itinerary. *Bull. Mus. comp. Zool.*, **79**: 479-541.

Lovett, J. C., 1988. – Endemism and affinities of the Tanzanian montane forest flora. *Monogr. Syst. Bot. Missouri Bot. Gard.*, **25**: 591-598.

----- 1990. – Classification and status of the moist forests of Tanzania. *Mitt. Inst. allg. Bot. Hamburg*, **23a**: 287-300.

Maley, J., 1996. – The African rain forest: main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quarternary. *Proc. r. Soc. Edinburgh*, **104B**: 31-73.

Noble, G. K., 1924. – Contributions to the herpetology of the Belgian Congo. *Bull. amer. Mus. nat. Hist.*, **49**: 147-347.

Olson, D. M. & Dinerstein, E., 1998. – The Global 200, a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conserv. Biol.*, **12**: 502-515.

Perret, J.-L., 1966. – Les Amphibiens du Cameroun. *Zool. Jb. (Syst.)*, **8**: 289-464.

----- 1988. – Sur quelques genres d'Hyperoliidae restés en question. *Bull. Soc. neuchât. Sci. nat.*, **111**: 35-48.

Poynton, J. C., 1962. – Geographical and ecological determinants of distribution patterns. *Ann. Cape Prov. Mus. nat. Hist.*, **2**: 32-36.

----- 1990. – Composition and subtraction patterns of the East African lowland Amphibian fauna. *In*: G. Peters & R. Hutterer (ed.), *Vertebrates in the tropics*: 285-296.

----- 1995. – The "arid corridor" distribution in Africa: a search for instances among Amphibia. *Madoqua*, **19**: 45-48.

----- 1998. – Introduction: Gladwyn Kingsley Noble and the study of African amphibians. *In*: K. P. Schmidt & G. K. Noble, *Contributions to the herpetology of the Belgian Congo*. Reprint edition, *Soc. Study Amph. Rept.*, Ithaca, N. Y.

----- 1999. – Distribution of Amphibians in Sub-Saharan Africa, Madagascar and the Seychelles. *In*: W. E. Duellman (ed.), *Patterns of distribution of Amphibia, a global perspective*: 483-533.

----- 2000*a*. – Evidence for an Afrotemperate amphibian fauna. *Afr. J. Herp.*, **49** (1): 33-41.

----- 2000*b*. – Amphibians of Coastal Forests. *In*: N. D. Burgess & G. P. Clarke (ed.), *Coastal forests of Eastern Africa*, IUCN.

Poynton, J. C. & Broadley, D. G., 1991. – Amphibia Zambesiaca. 5. Zoogeography. *Ann. Natal Mus.*, **32**: 221-277.

POYNTON, J. C., LOADER, S. P., SHERRATT, E. & CLARKE, B. P., 2006. – Amphibian diversity in an East African biodiversity hotspot: altitudinal and latitudinal patterns. *Biodivers. & Conserv.*: 1-15
RIVA, I. DE LA, 1994. – Anfibios anuros del Parque Nacional de Monte Alén, Rio Muni, Guinea Ecuatoreal. *Rev. esp. Herp.*, 8: 123-139
RÖDEL, M.-O., 2000. – *Amphibians of the West African savanna*. Chimaira: 1-332
----- 2003. – The amphibians of Marahoue and Mt. Peko National Parks, Ivory Coast. *Herpetozoa*, 16: 23-39
RÖDEL, M.-O., KOSUCH, J., VEITH, M. & ERNST, R. 2003. – First record of the genus *Acanthixalus* from the Upper Guinean Rain Forest, West Africa, with the description of a new species. *J. Herp.*, 37: 43-52
RÖDEL, M.-O. & AGYEI, A. C., 2003. – Amphibians of the Togo-Volta highlands, eastern Ghana. *Salamandra*, 39 (3-4): 207-234.
RÖDEL, M. O. & BRANCH, W., 2002. – Herpetological survey of the Haute Dodo and Cavally forests, western Ivory Coast. *Salamandra*, 38 (4): 245-268
RÖDEL, M.-O. & ERNST, R., 2001. – Redescription of the tadpole of *Phlyctimantis boulengeri*. *Alytes*, 18: 178-186.
RÖDEL, M.-O., GIL, M., AGYEI, A. C., LEACHÉ, A. D., DIAZ, R. E., FUJITA, M. K. & ERNST, R., 2005. – The amphibians of the forested parts of south-western Ghana. *Salamandra*, 41: 107-127
RÖDEL, M.-O., GRAFE, T. U., RUDOLF, V. H. W. & ERNST, R., 2002. – A review of West African Spotted *Kassina*. *Copeia*, 2002: 800-814.
SCHICK, S., VEITH, M. & LÖTTERS, S., 2005. – Distribution patterns of amphibians from the Kakamega Forest, Kenya. *Afr. J. Herp.*, 54 (2): 185-190
SCHIØTZ, A., 1967. – The treefrogs of West Africa. *Spolia zool. Mus. haun.*, 25: 1-346
----- 1975. – *The treefrogs of Eastern Africa*. Steenstrupia: 1-232
----- 1976. – Zoogeographical patterns in the distribution of East African treefrogs. *Zool. afr.*, 11 (2): 335-338
----- 1981. – The Amphibia of the forested basement hills of Tanzania, a biogeographical indicator group. *Afr. J. Ecol.*, 19: 205-207
----- 1999. – *Treefrogs of Africa*. Chimaira: 1-350.
----- 2006. – Notes on the genus *Hyperolius* in central République Démocratique du Congo. *Alytes*, 24 (1-4): 40-60
SCHIØTZ, A. & DAELE, P. V., 2003. – Notes on the treefrogs of North-Western Province, Zambia. *Alytes*, 20 (3-4): 137-149
SOSEF, M. S. M., 1994. – Refuge Begonias. *Studies in Begoniacea*, Univ. of Wageningen, 5.
SORENSEN, T. 1948. – A method of establishing groups of equal amplitude in plant sociology based on similarity of species contents and its application to analyses of the vegetation of a Danish commons. *Kgl. Danske Vid. Selskab., Biol. Skr.*, 5: 1-34
TINSLEY, R. C., LOUMONT, C. & KOBEL, H. R., 1996. – Geographical distribution and ecology. *In*: *The Biology of Xenopus*, *Symposia zool. Soc. London*, 68: 35-60
WHITE, F., 1993. – Refuge theory, ice-age aridity and the history of tropical biotas: an essay in plant geography. *Fragm. Flor. Geobot.*, Suppl. 2: 385-409
WIECZOREK, A. M., DREWES, R. C. & CHANNING, A., 2000. – Biogeography and evolutionary history of *Hyperolius* species: application of molecular phylogeny. *J. Biogeogr.*, 27: 1231-1243

Corresponding editor: Alain DUBOIS

APPENDIX 1

LIST OF TAXA MENTIONED IN THIS PAPER, ACCORDING TO THE FAMILIAL AND GENERIC TAXONOMY OF FROST ET AL. (2006)

Genus	Species and subspecies
Family *HYPEROLIIDAE* Laurent, 1943	
Acanthixalus Laurent, 1944	*sonjae* Rödel, Kosuch, Veith & Ernst, 2003, *spinosus* (Buchholz & Peters, 1875)
Afrixalus Laurent, 1944	*dorsalis dorsalis* (Peters, 1875); *dorsalis regularis* Laurent, 1951, *equatorialis* (Laurent, 1941); *fulvovittatus* (Cope, 1861); *lacteus* Perret, 1976, *laevis* (Ahl, 1930); *leucostictus* Laurent, 1950; *nigeriensis* Schiøtz, 1963, *osorioi* (Ferreira, 1906), *paradorsalis* Perret, 1960, *schneideri* (Boettger, 1889); *sylvaticus* Schiøtz, 1974; *uluguruensis* (Barbour & Loveridge, 1948); *vibekensis* Schiøtz, 1967
Alexteroon Perret, 1988	*hypsiphonus* Amiet, 2000, *jynx* Amiet, 2000, *obstetricans* (Ahl, 1931)
Arlequinus Perret, 1988	*krebsi* (Mertens, 1938)
Callixalus Laurent, 1950	*pictus* Laurent, 1950
Chlorolius Perret, 1988	*koehleri* (Mertens, 1940)
Cryptothylax Laurent & Combaz, 1950	*greshoffii* (Schilthuis, 1889), *minutus* Laurent, 1976
Hyperolius Rapp, 1842	*acutirostris* Buchholz & Peters, 1875, *adspersus* Peters, 1877, *alticola* Ahl, 1931; *baumanni* Ahl, 1931, *bobirensis* Schiøtz, 1967; *bolifambae* (Mertens, 1938); *bopeleti* Amiet, 1980, *brachiofasciatus* Ahl, 1931, *camerunensis* Amiet, 2004, *castaneus* Ahl, 1931; *chlorosteus* (Boulenger, 1915); *chrysogaster* Laurent, 1950; *cinnamomeoventris* Bocage, 1866, *concolor concolor* (Hallowell, 1844); *concolor ibadanensis* Schiøtz, 1967, *diaphanus* Laurent, 1972, *dintelmanni* Lötters & Schmitz, 2004; *endjami* Amiet, 1980; *ferrugineus* Laurent, 1943; *frontalis* Laurent, 1950, *fusciventris burtoni* (Boulenger, 1883), *fusciventris fusciventris* Peters, 1876, *fusciventris lamtoensis* Schiøtz, 1967, *ghesquieri* Laurent, 1943; *guttulatus* Günther, 1858, *hutsebauti* Laurent, 1956; *inornatus* Laurent, 1943, *kihangensis* Schiøtz & Westergaard, 1999, *kivuensis* Ahl, 1931, *kuligae* Mertens, 1940, *langi* Noble, 1924, *lateralis* Laurent, 1940, *laurenti* Schiøtz, 1967; *leleupi* Laurent, 1951, *leucotaenius* Laurent, 1950; *mitchelli* Loveridge, 1953, *mosaicus* Perret, 1959, *nasutus* Günther, 1865, *nienokouensis* (Rödel, 1998); *nimbae* Laurent, 1958, *occidentalis* Schiøtz, 1967, *ocellatus* Günther, 1858, *pardalis* Laurent, 1948, *phantasticus* (Boulenger, 1899); *picturatus* Peters, 1875; *platyceps* (Boulenger, 1900), *puncticulatus* (Pfeffer, 1893), *riggenbachi hieroglyphicus* Ahl, 1931, *riggenbachi riggenbachi* (Nieden, 1910); *robustus* Laurent, 1979, *rubrovermiculatus* Schiøtz, 1975, *sankuruensis* Laurent, 1979, *spinigularis* Stevens, 1971, *sylvaticus ivorensis* Schiøtz, 1967; *sylvaticus nigeriensis* Schiøtz, 1967, *sylvaticus sylvaticus* Schiøtz, 1967, *tannerorum* Schiøtz, 1982, *torrentis* Schiøtz, 1967, *tuberculatus* (Mocquard, 1897), *viridiflavus* (Duméril & Bibron, 1841); *viridigulosus* Schiøtz, 1967, *wermuthi* Laurent, 1961, *xenorhinus* Laurent, 1972, *zonatus* Laurent, 1958
Kassina Girard, 1853	*arboricola* Perret, 1985, *cochranae* (Loveridge, 1941); *decorata* (Angel, 1940); *lamottei* Schiøtz, 1967; *maculosa* (Sternfeld, 1917) *mertensi* Laurent, 1952, *schioetzi* Rödel, Grafe, Rudolf & Ernst, 2002
Opisthothylax Perret, 1966	*immaculatus* (Boulenger, 1903)
Phlyctimantis Laurent & Combaz, 1950	*boulengeri* Perret, 1986; *keithae* Schiøtz, 1975, *leonardi* (Boulenger, 1906), *verrucosus* (Boulenger, 1912)

APPENDIX 1 (continued)

Genus	Species and subspecies
Family *ARTHROLEPTIDAE* Mivart, 1869	
Arthroleptis Smith, 1849	
Astylosternus Werner, 1898	*batesi* (Boulenger, 1900); *diadematus* Werner, 1898
Cardioglossa Boulenger, 1900	*gratiosa* Amiet, 1972, *nigromaculata* Nieden, 1908
Leptodactylodon Andersson, 1903	*albiventris albiventris* (Boulenger, 1905), *albiventris bueanus* Amiet, 1981, *ovatus* Andersson, 1903, *ventrimarmoratus* (Boulenger, 1904)
Leptopelis Günther, 1859	*aubryi* (Dumeril, 1856); *barbouri* Ahl, 1929; *boulengeri* (Werner, 1898); *brevirostris* (Werner, 1898); *calcaratus calcaratus* (Boulenger, 1906); *calcaratus meridionalis* Laurent, 1973; *christyi* (Boulenger, 1912); *crystallinoron* Lötters, Rödel & Burger, 2005, *fenestratus* Laurent, 1972; *fiziensis* Laurent, 1973, *flavomaculatus* (Günther, 1864), *hyloides* (Boulenger, 1906); *kivuensis* Ahl, 1929, *mackayi* Köhler, Bwong, Schick, Veith & Lötters, 2006, *macrotis* Schiøtz, 1967, *millsoni* (Boulenger, 1895), *modestus* (Werner, 1898); *notatus* (Peters, 1875), *occidentalis* Schiøtz, 1967, *ocellatus ocellatus* (Mocquard, 1902), *ocellatus schiotzi* Laurent, 1973; *omissus* Amiet, 1992; *parkeri* Barbour & Loveridge, 1928, *rufus* Reichenow, 1874; *uluguruensis* Barbour & Loveridge, 1928; *vermiculatus* (Boulenger, 1909); *zebra* Amiet, 2001
Family *BUFONIDAE* Gray, 1828	
Bufo Laurenti, 1768	–
Family *PIPIDAE* Gray, 1828	
Xenopus Wagler, 1827	-
Family *PTYCHADENIDAE* Dubois, 1987	
Ptychadena Boulenger, 1917	-
Family *PHRYNOBATRACHIDAE* Laurent, 1941	
Phrynobatrachus Günther, 1862	-
Family *RHACOPHORIDAE* Hoffman, 1932 (1858)	
Chiromantis Peters, 1854	*rufescens* (Günther, 1869)

APPENDIX 2

COMPARISON OF TERMINOLOGY BETWEEN THIS PAPER, WWF'S GLOBAL 200 (OLSON & DINERSTEIN, 1998) AND POYNTON (1999)

Present treatment	Global 200	POYNTON, 1999
Liberia (block 1) + Gold Coast (block 2) + Trans-Volta -Togo (block 3)	Guinean Moist Forests	Western province of West Equatorial Region
Southern Nigeria (block 4)	No separate ecoregion	Central, East and South Province of West Equatorial Region
Cross-Sanaga Coastal Forests (block 5)	Northwestern part of Congolian Coastal Forests	
Congolian Coastal Forests (block 6)	Southern part of Congolian Coastal Forest	
North-western Congolian Forests (block 7)	Western Congo Basin Moist Forests	Not congruent with subdivisions of WWF
Central Congolian Forests (block 8)	Central Congo Basin Moist Forests	
North-eastern Congolian Forests (block 9)	North-eastern Congo Basin Moist Forests	
Eastern Forests (block 10)	Eastern Arc Montane Forests + East African Coastal Forests	Eastern province of Intertropical Montane Region + East Coast Forests + Forested parts of eastern Coast Lowlands

Appendix 3

Notes on problematic species

A number of treefrogs, especially from Central Africa, have unknown habitat preferences and are therefore omitted here. They are *Cryptothylax minutus*, *Hyperolius brachiofasciatus*, *H. chrysogaster*, *H. diaphanus*, *H. ferrugineus*, *H. inornatus*, *H. leucotaenius*, *H. sankuruensis*, *H. xenorhinus* and *Leptopelis fenestratus*.

A group of treefrogs seems to prefer habitats which are intermediary between sylvicolous and parasylvicolous, and reference to either of these categories can be disputed. It is my impression that such species do not generally have broader habitat requirements, being more generalised than others, but are rather "in between", preferring dense vegetation in parasylvicolous habitats or open vegetation in sylvicolous habitats. *Hyperolius sylvaticus*, *Kassina cochranae*, *K. arboricola* and *Phlyctimantis boulengeri* were with reservations referred to as sylvicolous by Schiøtz (1967). Here, partly based on the extensive field knowledge of Rödel (in litt.), they are termed parasylvicolous although found in denser vegetation in this habitat type. Similarly, Amiet (1986) has listed *Acanthixalus spinosus*, *Afrixalus paradorsalis*, *Hyperolius kuligae*, *H. ocellatus* and *H. platyceps* as occasionally occurring in both habitats. The preferred habitat is used here.

The so-called *Afrixalus fulvovittatus* group (Schiøtz, 1999) (striped *Afrixalus*) has an unsettled and confused taxonomy, probably consisting of several species, some savanicolous, others parasylvicolous. The parasylvicolous form in western West Africa (*A. fulvovittatus* sensu stricto) seems well defined in westernmost Africa, but Rödel et al. (2005) mentioned the possible occurrence of this species in south-western Ghana. Rödel & Pickersgill (in litt.), however, raised doubts about the identity of the eastern samples. A photo by Leaché sent to me by Pickersgill (from Ankassa, Ghana) is of *A. dorsalis* with a middorsal stripe. In Cameroun and Central Africa the situation is unsettled. This complex is disregarded here.

Afrixalus schneideri is an enigmatic species with a characteristic morphology which could indicate that it is the Cameronese representative of a group of large sylvicolous *Afrixalus* including *A. equatorialis*, *A. leucostictus* and *A. nigeriensis*, but only one specimen is known, from a very well explored part of Cameroun.

Hyperolius spinigularis has an enigmatic habitat preference, being apparently found both in dense forest and in very open farmland, but so inconspicuous and therefore easily overlooked that distribution cannot be given. Most records are above 1000 m. The species is omitted in this study.

Hyperolius langi is omitted since its habitat preference and taxonomy are badly understood especially in relation to *H. kuligae* and *H. platyceps*. Doubtful records from Uganda (Schiøtz, 1999, as *H. kuligae*) may be *H. langi*.

Hyperolius cinnamomeoventris is the only *Hyperolius* assumed to be both parasylvicolous and savanicolous. Only parasylvicolous populations are dealt with here, as this name might possibly cover several species.

Spotted *Kassina* from forest regions form a parasylvicolous group with an unsettled taxonomy. In West Africa, Rödel et al. (2002) revised the group, and two members, *K. arboricola* and *K. cochranae* are included in this study. The third West African species, *K. schioetzi*, is omitted because of uncertainty about its habitat affinity. Further east the situation is unsettled. In the well investigated Cameroun, several taxa seem to be confused under the name *K. maculosa* or *K. decorata*. Further east, available material is insufficient. The spotted forest kassinas from Central Africa are therefore omitted.

Leptopelis modestus has a doubtful taxonomy. Possibly four taxa are involved: from Cameroun possibly two taxa with slightly different morphologies from montane forests (eastern Nigeria and western Cameroun) and lowland forests (the latter harbouring the type locality), furthermore recorded from eastern Congo and from western Kenya, the latter population having recently been described as *L.*

mackayi Only the Cameronese populations of *L. modestus* and *L. mackayi* are treated here, the eastern Congo populations omitted

Phlyctimantis boulengeri occurs in the Liberia block and in the westernmost Gold Coast block, and then, after a hiatus of 1000 km, in easternmost Nigeria and in Cameroun Being a conspicuous species, it was probably not overlooked in between There is suspicion that the two populations, "*P boulengeri* W" and "*P boulengeri* E" are two different taxa (RÖDEL & ERNST 2001, SCHIØTZ, 1999), therefore the two populations are treated here as separate taxa.

APPENDIX 4

ALTITUDINAL RANGES OF SPECIES IN BLOCK 10

Data were kindly provided by POYNTON (in litt) and supplemented with my own data

200 m is the lowest investigated altitude with closed canopy moist forest (east slopes of Eastern Usambaras)

PARASYLVICOLOUS SPECIES

Hyperolius mitchelli 10-1050 m
Hyperolius puncticulatus: 10-2100 m
Leptopelis flavomaculatus : 10-1370 m
Phlyctimantis keithae: 1840-1950 m.

SYLVICOLOUS SPECIES

Afrixalus uluguruensis : 750-1740 m.
Hyperolius kihangensis: 1410 m.
Hyperolius tannerorum: 1740 m.
Leptopelis barbouri: 1000-1740 m.
Leptopelis parkeri: 410-1740 m
Leptopelis uluguruensis: 200-1250 m
Leptopelis vermiculatus: 200-1410 m